

FOOD AND FEEDING HABITS OF AUTUMN MIGRANT SHOREBIRDS AT A SMALL MIDWESTERN POND

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MOST shorebirds in migration traverse so great a distance and so many ecologically different areas that it is improbable that they are able to maintain a very specific diet. Whereas they might feed, for example, mainly on certain dipteran larvae on the breeding grounds, they may not find these available during migration. Thus they must turn to other types of food and broaden their feeding niches. This may cause greater dietary overlap and competition between species.

Although some overlap is to be expected, there are differences in the basic feeding patterns and size differences which preclude total overlap between species. It is the purpose of this study, besides adding to the sparse knowledge of foods of migrating birds, to demonstrate that while there is considerable overlap in the diets of several species of shorebirds during autumn migration, there are differences which indicate at least partial segregation into different feeding niches.

The data were gathered in conjunction with a migration study done in 1960 and 1961. Observations were made and sampling was done at a shallow mud-bottom pond approximately $\frac{1}{4}$ mile north of Champaign, Illinois. This was apparently the only suitable feeding place for shorebirds in the area, and it is probable that the birds collected had consumed their food there.

METHODS

Varying numbers of nine of the 20 species under observation were collected with a shotgun for stomach analysis during the autumn migration: Common Snipe (*Capella gallinago*), 5 in October, 1961; Greater Yellowlegs (*Totanus melanoleucus*), 2 in October, 1960, one in November, 1961; Lesser Yellowlegs (*Totanus flavipes*), 4 in September and 2 in October, 1960, 3 in October, 1961; Pectoral Sandpiper (*Erolia melanotos*), 2 in October, 1960, and 1 in October, 1961, 4 in July, 1961; Least Sandpiper (*Erolia minutilla*), 1 in October, 1960, 3 in July, 1961; Dunlin (*Erolia alpina*), 2 in October, 1961; Stilt Sandpiper (*Micropalama himantopus*), 2 in October, 1960; Semipalmated Sandpiper (*Ereunetes pusillus*), 2 in August, 1961; Wilson's Phalarope (*Steganopus tricolor*), 1 in July, 1961.

The digestive tract was removed no later than one hour after death and preserved in 70 per cent ethanol. The contents of esophagus, proventriculus, and ventriculus were later emptied into a shallow dish and the parts of each type of food organism separated into groups using a binocular dissecting

microscope. The number of organisms making up each group and the percentage that these made up of the total number of organisms in the stomach was then determined. In the cases where it was considered that plant material was purposefully ingested the percentage by bulk of this material was estimated, and the percentage of other organisms calculated on the remainder, as above.

The pond bottom was sampled throughout the year to determine the kinds and numbers of benthic organisms available to the birds by pushing a brass cylinder of 0.0077 m² area into the substrate to a depth of 10–15 cm, washing the contents through a 1.5 mm mesh sieve, and counting the organisms. Sampling locations were randomly selected in water 15 cm or less deep in the general areas where the birds fed. Varying numbers of samples were taken 2 to 4 times a month during migrations, and once a month at other times of the year.

Mats of filamentous algae formed over much of the pond's surface in late summer and autumn, creating a new feeding substrate for the smaller shorebirds in particular. Free-swimming, algal-mat, and shoreline food organisms were not sampled quantitatively but relative numbers were established by observation on the days when bottom samples were taken.

RESULTS AND DISCUSSION

In addition to the benthic organisms (Table 1), northern fathead minnows (*Pimephales promelas*: Cyprinidae) and numerous free-swimming adult aquatic beetles were present. Relative numbers of the fish could not be determined but, of the insects, Dytiscidae made up approximately 50 per cent, Haliplidae (crawling water beetles), 30 per cent, and Hydrophilidae, 20 per cent. Their relative numbers did not appear to change significantly during the migration period. Other aquatic insects were present but in very small numbers. Non-aquatic insects made up about 60 per cent of the available shoreline and algal-mat organisms during the entire migration period. stratiomyid (soldier fly) larvae, 30 per cent, and haliplid larvae, 10 per cent. Terrestrial insects of various species were commonly found trapped on the water surface, and wind-blown concentrations were often found against and on the algal mats.

Specificity of diet concerns the number of different food items consumed by a species. By these terms the Lesser Yellowlegs would be least, and the Stilt Sandpiper most specific (Tables 2 and 3), but the small and unequal sample sizes do not permit any conclusion here. It is probable that the larger species are less specific than the smaller ones, since they are not as restricted to the shoreline or to relatively smaller organisms.

TABLE I
DENSITIES¹ OF BENTHIC ORGANISMS

Organism	Jan. (3) ²	Feb. (2)	Mar. (4)	Apr. (7)	May (4)	June (3)	July (7)	Aug. (11)	Sept. (15)	Oct. (8)	Nov. (4)	Dec. (2)
Physidae (snails)	130	65	130	334	1,203	650	1,021	1,076	966	748	390	130
Chironomidae (midge flies)												
larvae, pupae	173	—	195	111	293	130	111	166	337	211	98	65
Diptera (flies)												
larvae, pupae	87	—	228	74	163	216	74	142	57	33	131	65
Corixidae (water boatmen)	—	—	163	56	98	43	37	154	61	98	98	—
Baetidae (may- flies) naiads	—	—	—	—	33	43	56	59	132	65	—	—
Hydrophilidae (water scav- enger beetles)												
larvae	—	—	—	—	65	43	56	24	20	16	—	—
Anisoptera (dragonflies)												
naiads	—	—	—	19	65	43	—	12	1	16	—	—
Coenagrionidae (damselflies)												
naiads	—	—	—	—	33	43	—	12	—	—	—	—
Dystiscidae (predaceous diving beetles)												
larvae	—	—	—	—	—	43	—	24	—	16	—	—

1 Individuals per m².

2 Number of samples.

Selectivity of diet concerns the relation between the quantity of a certain food item available and the quantity consumed. The forage ratio of Hess and Swartz (1941), calculated by dividing the per cent of a food item in the stomach by the per cent of that item in the fauna, gives a measure of the selectivity of an animal for the components of its diet. A value of less than unity denotes that the item is not selected in relation to its abundance; unity, that it is selected in direct relation to its abundance; greater than unity, that it is selected out of proportion to its abundance or that it is a preferred item. The forage ratios (Tables 2 and 3) show that most of the species were apparently selective for several items in their diets but had at least one item of high preference peculiar to each.

Lack (1945) concluded that closely related species differ in one or more of the following: habitat, region, or diet. Two closely related phalacrocora-

cids, very similar in appearance, habitat, and region "differ markedly in both nesting sites and food." Dietary selectivity is the major differing factor in the niches of these species which can account for their coexistence without contradicting Gause's rule. He found (1944) that in many closely related sympatric passerines dietary differences were important in their ability to coexist. This is now a rather well-known ecological fact, but his and others' observations have concerned only breeding or permanent resident birds. Lack stated (1944:276) that "closely related species are potential food competitors in winter, and so have evolved geographical isolation at this season . . .," and suggested that off the breeding grounds (during migration and on the wintering grounds) their food may become more similar. The results of the present study, however, indicate that the identities of separate feeding niches may be maintained through migration, or, in light of Holmes' (1964) finding, that the feeding niches of congeneric species of sandpipers almost completely overlapped during the breeding season, the niches may even become more divergent.

Competition should be greater for preferred food items than for others. In cases where two or more species shared a high preference, they usually did not compete, because their feeding areas were different. However, during the peak of migration, in early September both years, competition should have been and apparently was keenest between species which had common preferred food items and common feeding areas. Lesser Yellowlegs and Pectoral Sandpipers (the first and second ranked species at the pond with respective 4-month averages of 14 and 12 birds seen per trip to the area and peak numbers of 125 and 50) both selected hydrophilid larvae, and aggressive encounters between these two species were the only ones seen, being most noticeable in early September. Close study was not made of this behavior, and although Hamilton's (1959) "crouch" and "supplanting" displays by Pectoral Sandpipers were the only ones noticed, there were no doubt other aggressive displays that I did not recognize. This behavior was shown usually between Pectoral Sandpiper individuals, less often between these and Lesser Yellowlegs, with the former being the apparent aggressor. The Least Sandpiper also selected hydrophilid larvae but no aggressive displays were noted involving this species, although less obvious displays, sufficient to cause the smaller species to move away without apparent conflict, could have been employed by the larger sandpipers.

No encounters between Stilt Sandpipers and Lesser Yellowlegs were observed, although they both selected chironomid larvae and corixids. Either the supply was sufficient or the fact that the former habitually fed in deeper water may have eliminated competition. There was no competition for chironomids between Lesser Yellowlegs and Least Sandpipers, since the

TABLE 2
FOOD HABITS OF THE SHORELINE-FREQUENTING SHOREBIRDS

Food item	Common Snipe			Pectoral Sandpiper						Least Sandpiper			Dunlin			Semipalmated Sandpiper		
	October (5) ¹			July (4)			October (2)			July (3)			October (2)			August (2)		
	F ²	D ³	FR ⁴	F	D	FR	F	D	FR	F	D	FR	F	D	FR	F	D	FR
<i>Benthic</i>																		
Phyidae	20	2	<0.1	100	52	0.7	50	1	<0.1	66	11	1.4	100	3	0.1	50	3	<0.1
Chironomidae				25	+	<0.1				33	1	1.0						
Diptera	20	+	<0.1							33	1	0.2						
Corixidae							50	25	25.0	100	7	1.8				50	4	4.0
Hydrophilidae	20	+	<0.1	25	3	0.8				33	1	1.0						
Dytiscidae																		
<i>Free-swimming</i>																		
Dytiscidae	80	21	0.4	75	9	0.2	50	25	0.5	100	14	0.3	100	8	0.2	50	3	0.1
Hydrophilidae				75	6	0.3				66	10	0.5	100	58	2.9	50	4	0.2
<i>Shore, Algal Mat</i>																		
Insects, misc.							50	7	0.1	66	2	<0.1	100	16	0.3			
Stratiomyidae	20	20	0.7				50	42	1.4	66	43	1.4	100	14	0.5			
Halipidae	20	2	0.2	25	17	1.7				33	10	1.0						
<i>Plant Material</i>																		
Algae	60	43	-													100	86	-
Seeds	100	12	-	75	13	-	50	1	-				100	3	-			

1 Sample size.
 2 Frequency, per cent of stomachs containing item.
 3 Per cent of item in diet.
 4 Forage ratio, values > 1 in boldface.

TABLE 3
FOOD HABITS OF THE SHOREBIRDS FEEDING AWAY FROM SHORE

Food item	Greater Yellowlegs						Lesser Yellowlegs						Stilt Sandpiper						
	October (2) ¹		November (1)		September (4)		October (5)		October (2)		F	D	FR	F	D	FR			
	F ²	D ³	FR ⁴	F	D	FR	F	D	FR	F							D	FR	F
<i>Benthic</i>																			
Physidae				100	25	0.5				50	4	0.1							
Chironomidae				100	35	1.7				100	35	1.7				100	46	2.6	
Diptera										25	+	<0.1							
Corixidae				100	2	0.2				75	20	5.0				100	59	7.4	
Baetidae										25	10	1.3				20	8	1.6	
Hydrophilidae										75	6	5.5				40	3	3.0	
Anisoptera				100	88	2.8										60	10	0.3	
Coenagrionidae																20	1	1.0	
<i>Free-swimming</i>																			
Dytiscidae										50	23	0.7				60	17	0.3	
Hydrophilidae										25	1	0.1							
Cyprinidae				50	12	-				100	5	-							
<i>Shore, Algal Mat</i>																			
Insects, misc.										25	+	<0.1				60	2	0.1	
Stratiomyidae																20	+	<0.1	
<i>Plant Material</i>																			
Seeds				100	3	-				25	+	-							

1 Sample size.

2 Frequency, per cent of stomachs containing item.

3 Per cent of item in diet.

4 Forage ratio, values > 1 in boldface.

former generally probed the bottom and the latter took only pupae which had come to the surface and were washed ashore or against the algal mats.

It is possible that the aggressive behavior described above was not due to active competition for a food item but to the preservation by the birds of their "individual distances." Hamilton (1959) reports that when this distance is reached, threatening usually occurs among Pectoral Sandpipers. However, he did not mention that this occurred interspecifically in the general feeding area, and for this reason active competition cannot be excluded as being responsible for the aggressive behavior shown between species in the present study.

Several species examined had eaten considerable plant material. Forage ratios could not be calculated for this type of food but the high frequencies and percentages of seeds taken by the Common Snipe and Pectoral Sandpiper, and of algae by the snipe and Semipalmated Sandpiper indicate that they were selecting this over animal food in some instances. Plant material was present in almost all stomachs examined but was usually in very small amounts and was considered to have been taken incidentally with animal food by all except the species mentioned above.

Of interest is that while adult halipid beetles composed about 30 per cent of the free-swimming fauna, not one was found in the stomachs. The reason for their apparent unpalatability may be that they have an extremely thick and hard external covering and are very resistant to crushing. If they cannot be crushed they obviously have little food value.

Little correlation can be made between temporal changes in densities of food organisms, number of birds present, and dietary changes of the birds, due to the relatively small number of stomachs examined. Forage ratios should reflect a change of any sort (or no change) when comparing a species of shorebird at different times. The Lesser Yellowlegs, for which the most samples are available, is taken as an example. Of those food items for which the ratio was greater than unity in either September or October (see Table 3) the density of hydrophilid larvae decreased about 20 per cent, mayfly naiads, 50 per cent, and chironomid larvae and pupae, 33 per cent, while corixids increased about 33 per cent. The respective forage ratios decreased about 50 per cent, increased 20 per cent, decreased 100 per cent, and increased about 33 per cent. Although the data do not permit a conclusion, it is attractive to speculate that as the density of one preferred organism decreases, the birds feed more intensively on another preferred organism for which the density has increased. This, of course, follows the established ecological principle that as a population decreases or increases, external pressures such as predation tend to decrease or increase with it.

The size of the bird, or more accurately, the leg-length, appeared to in-

fluence the food of the different species. The smaller or short-legged species usually did not feed in deeper water, taking organisms available on the shore, the algal mats, or in very shallow water. Greater numbers of free-swimming and terrestrial forms were consumed by them, in contrast to the larger species, which took more benthic organisms (see Tables 2 and 3 respectively). It should be mentioned here that the Least Sandpiper collected in October and the Wilson's Phalarope in July, omitted in the tables, had eaten only non-aquatic insects.

On the basis of the food habits, general size of the birds, main feeding sites, and tendency to feed together, the 20 species present at the pond during the study can be placed into three feeding groups:

Group I. Larger species which fed exclusively on the shore:

Killdeer (*Charadrius vociferus*), American Golden Plover (*Pluvialis dominica*), Black-bellied Plover (*Squatarola squatarola*), Buff-breasted Sandpiper (*Tryngites subruficollis*).

Group II. Smaller or short-legged species which fed on or near the shore or on the algal mats:

Semipalmated Plover (*Charadrius semipalmatus*), Common Snipe, Spotted Sandpiper (*Actitis macularia*), Pectoral Sandpiper, Baird's Sandpiper (*Erolia bairdii*), Least Sandpiper, Dunlin, Semipalmated Sandpiper, Western Sandpiper (*Ereunetes mauri*), Sanderling (*Crocechia alba*).

Group III. Larger species which fed most commonly in water up to belly-deep:

Solitary Sandpiper (*Tringa solitaria*), Greater Yellowlegs, Lesser Yellowlegs, Short-billed Dowitcher (*Limnodromus griseus*), Stilt Sandpiper, Wilson's Phalarope.

There were individual exceptions, but as a rule these groups were distinguishable in the field. A zonation was evident, with Group I at the periphery, Group II near the water's edge, and Group III located out in the water. The Lesser Yellowlegs was ubiquitous but more often fed in deeper water away from shore. It has been somewhat arbitrarily placed in Group III rather than in Group II.

The Wilson's Phalarope possibly should be grouped by itself. Although it fed with the others of Group III, the specimen collected had consumed 100 per cent non-aquatic insects, as mentioned above. Apparently it took floating insects from the surface of the water and from algal mats, unlike the others.

SUMMARY

The general feeding habits of 20 species of shorebirds at a small pond near Champaign, Illinois, were observed and stomach analyses of nine of these species were made

during the autumn migrations of 1960 and 1961. The numbers and kinds of available food organisms at the pond were established by quantitative sampling of benthic invertebrates and estimation of relative numbers of free-swimming and shoreline organisms.

Although most species did not show dietary specificity, consuming a rather wide array of organisms, all showed dietary selectivity, in that one or a few of the food items were sought out over the others and out of proportion to their abundance. Competition was probably reduced by this selectivity, and where two species shared high preference for the same item, competition was alleviated by the fact that they usually fed at different sites.

Aggressive behavior was observed intraspecifically with the Pectoral Sandpiper, and at the peak of migration, interspecifically between these and Lesser Yellowlegs. They may have been actively competing for a preferred food item common to both.

The Common Snipe, Pectoral Sandpiper, and Semipalmated Sandpiper appeared to consume considerable amounts of plant material intentionally. The other species probably took it incidentally with animal food.

The size or leg-length of the bird partially determined its diet. Small species were apparently unable to forage in deeper water or ingest large organisms.

The 20 species were placed into three groups on the basis of their food, general size, main feeding sites, and tendency to feed together. These groups, when feeding, were distinguishable in the field because of their evident zonation.

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